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ABIOTIC DIFFERENCES BETWEEN GREEN TURTLE (*CHELONIA MYDAS*) NESTS IN
NATURAL BEACH AND ENGINEERED DUNES: EFFECTS ON HATCHING SUCCESS

by

MARTHA ELIZABETH BALFOUR
B.S. University of Central Florida, 2004

A thesis submitted in partial fulfillment of the requirements
for the degree of Master of Science
in the Department of Biology
in the College of Sciences
at the University of Central Florida
Orlando, Florida

Summer Term
2010

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ABSTRACT

Habitat loss is among the biggest threats to conservation worldwide, so habitat restoration plays an increasing role in endangered species management. This is especially true for species with high site fidelity, such as nesting marine turtles. Sand replenishment is commonly used to restore coastal beaches after severe erosion events, and may affect marine turtles and other species that live or reproduce in that habitat. I investigated how abiotic characteristics of sand used in a dune restoration project at Archie Carr National Wildlife Refuge, Florida, affected reproduction of the federally-endangered green turtle (*Chelonia mydas*). Sand structure and composition can affect egg development and hatching success by altering nest conditions, with nests in fine-grain or very coarse sand suffering decreased hatching success. I determined that calcium carbonate content ($27.0\% \pm 1.4$ SE vs. $15.1\% \pm 3.8$ SE), moisture content ($3.29\% \pm 0.26$ SE vs. $4.59\% \pm 0.25$ SE), and grain size ($427.53 \mu\text{m} \pm 14.1$ SE vs. $274.66 \mu\text{m} \pm 29.1$ SE) differed significantly between natural and restored dunes. Hatching success of green turtles ($44.7\% \pm 6.2$ SE vs. $65.8\% \pm 5.3$ SE) was significantly lower on restored dunes compared to natural dunes with an estimated loss of 22,646 hatched eggs. Hatching success also decreased as the nesting season progressed. These results demonstrate the importance of regulating fill material used in beach restoration projects; substrate characteristics are easily evaluated and can significantly influence marine turtle hatching success.

I dedicate this work to my mother and father who *patiently* encouraged me every step of
the way.

ACKNOWLEDGMENTS

I acknowledge my major advisor, Dr. Llewellyn Ehrhart for teaching me so much about marine turtle biology and the value of getting your hands dirty to really understand the system in which you work. I thank my co-advisor, Dr. John Fauth, for all of his advice and extensive edits during the writing process. And I also acknowledge Dr. John Weishampel for his suggestions and support. The laboratory component of my thesis could not have been completed without the help of Drs. Fauth, Jenkins and Stout. I am very grateful for the use of their equipment and laboratories. Without those that helped me in the field and spent many a sleepless night with me on the beach, this work would have been difficult to bear: Jennifer Pudewell, April Verpoorten, Camille Brescacin - Collins, Hilary Suresch, Dean Bagley, Shaun Hirsch, and Tracy Thompson. I acknowledge the advice and kind encouragement I received from the late Boyd Lyon, whose passion for marine turtle conservation and research was inspiring. I acknowledge the great advice and support I received from Mary Beth Manjerovic, Cheryl Pinzone, Simona Ceriani and the Biology Graduate Student Association. I also acknowledge the advice I received from Mario Moto and Ray Carthy on this study and the data provided by Mike McGarry and Virginia Barker. I also thank Brandon Barton for his many edits and enduring encouragement throughout this process as well.

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LIST OF ABBREVIATIONS

ACNWR	Archie Carr National Wildlife Refuge
ANOVA	Analysis of Variance
HS	Hatching Success
MANOVA	Multivariate Analysis of Variance
SE	Standard Error

CHAPTER ONE: INTRODUCTION

Habitat degradation is a serious threat to endangered and threatened species (Sisk et al. 1994, Crain et al. 1995, Wilcove et al. 1998, Main et al. 1999, Kamel and Mrosovsky 2006), making habitat restoration an integral component of conservation and management (Frazer 1992). However, many habitats used by endangered, threatened and sensitive species also are used by humans (Sanderson et al. 2002). Consequently, restoring habitats for protected species requires careful planning and cooperation among stakeholders to meet the demands of both wildlife and humans (Hatch et al. 2002). This is especially true in coastal areas where human recreation and residences overlap with critical nesting habitats for threatened and endangered marine turtle species.

Archie Carr National Wildlife Refuge (ACNWR) was established in 1991 to conserve critical nesting habitat for three species of marine turtles, the leatherback (*Dermochelys coriacea*), loggerhead (*Caretta caretta*) and green turtle (*Chelonia mydas*) and to provide habitat for other endangered species across 33 km of Florida's east coast (Figure 1). Green turtle nesting at ACNWR was almost nonexistent (< 100 nests) in the early 1980's and has grown an average of 14% annually, totaling more than 3000 nests in 2005 (Chaloupka et al. 2008). Approximately 3/4 of the land within ACNWR is privately owned and several public parks are located within its boundaries. Consequently, ACNWR's beach is a recreational resource for local residents and visiting tourists (McGarry 2007, U.S. Fish and Wildlife Service 2008), contributing to a multimillion dollar ecotourism industry within Brevard County, FL (U.S. Fish

and Wildlife Service 2008). Thus, protecting beach is critical for both marine turtle conservation and the local economy.

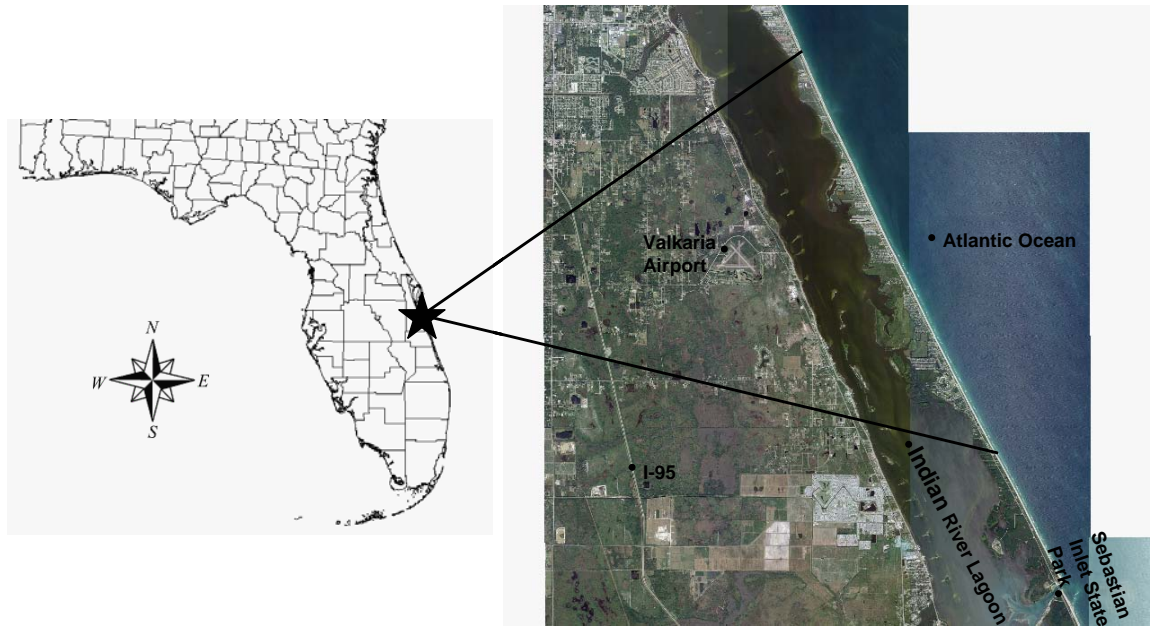


Figure 1. Archie Carr National Wildlife Refuge is located on Florida's east coast. The enlarged aerial image shows the 14.5 km section of beach examined during this study.

In 2004, a series of strong hurricanes eroded coastal dunes and damaged private residences and properties along the ACNWR coast. Beachfront properties were left with little to no protection from high surf. To prevent further damage and protect private property, Florida's Department of Environmental Protection permitted Brevard County government to import fill material and construct artificial dunes along developed portions of the refuge, leaving the remaining one fourth natural. Characteristics of beach substrate can substantially affect coastal wildlife, therefore Florida Department of Environmental Protection regulates fill material to ensure that it exhibits similar grain size distribution, color and carbonate content to existing sand, and does not contain materials not naturally found on the beach. Normally, dune restoration

projects minimize differences between natural sand and fill material by procuring substrates from nearby offshore borrow pits, inlets or channels (Crain et al. 1995). However, due to the immediate threat of further property loss, the 2005 ACNWR restoration project was allowed to acquire sand from the quickest source: inland quarries (Figure 2). Consequently, there was much concern that restored dunes differed from natural dunes and provided less suitable nesting habitats for marine turtles.

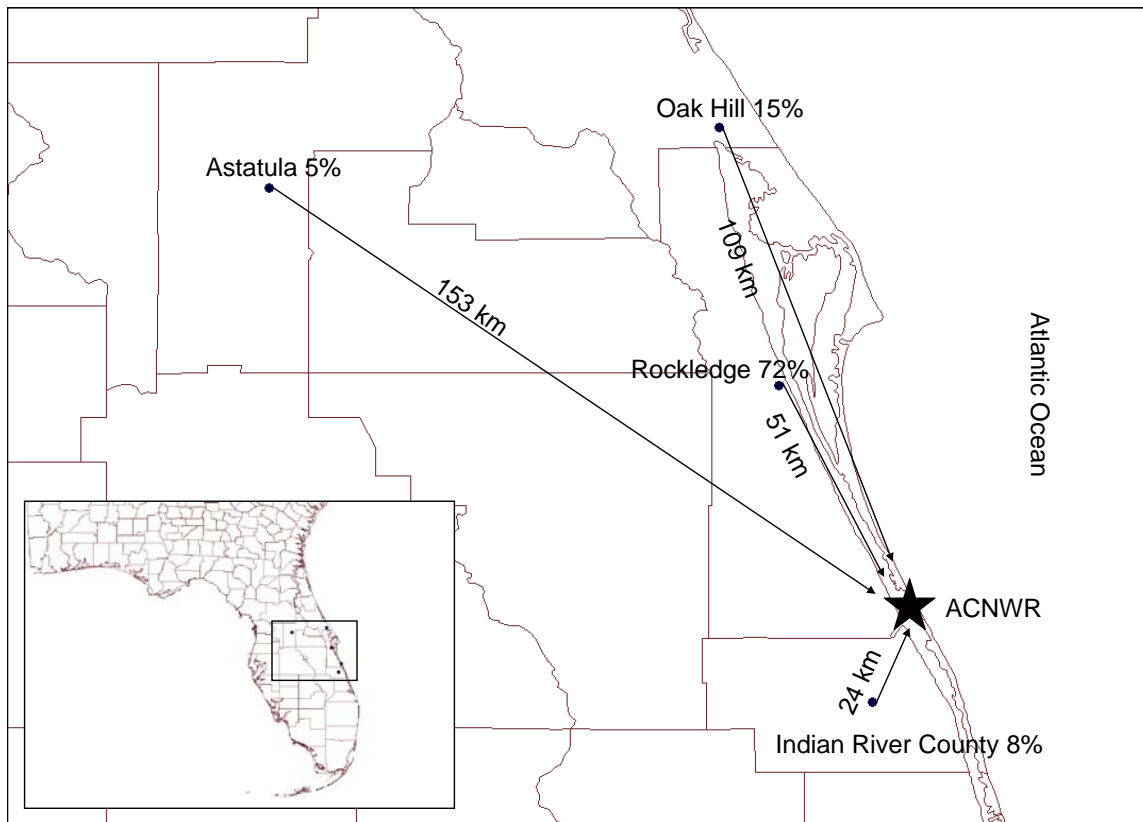


Figure 2. Fill material was obtained from quarries located 24 – 153 km from Archie Carr National Wildlife Refuge, FL, USA.

Physical characteristics of nesting medium determine the quality of a beach as marine turtle nesting habitat. Nest site selection and the ability of green turtles to dig an egg chamber are affected by sand compactness, porosity and moisture (Bustard and Greenham 1968, Chen et al. 2007). Grain size and shape, silt-clay content, color, moisture and porosity can affect turtle

embryonic development and hatchling production (Nelson 1992). Sand color alters the temperature found in tests with temperatures increasing as the color of sand darkens (Blair et al. 2000). The chemical environment of the sand also is important for organisms that use the beach (Bustard and Greenham 1968) and can be especially important for marine turtles, whose porous, parchment-like eggshells allow water and gas exchange between the environment and the developing embryo (Gans and Huey 1987). Calcium found in the sand may be absorbed through the eggshell for use by the developing turtle embryo (Bustard and Greenham 1968, Bilinski et al. 2001), making the chemical composition of sand an important consideration for beach restoration. Calcium uptake in embryonic turtles is negatively affected by increased moisture in the substrate (Bilinski et al. 2001), and wet substrates decreased loggerhead turtle (*Caretta caretta*) size and hatching success (McGehee 1990). Porosity affects gas availability; decreased gas availability slows embryonic growth, resulting in increased incubation periods and lower hatching success (Ackerman 1981).

Most studies of beach nourishment projects examined the loggerhead turtle (*Caretta caretta*), which is the most common species nesting in Florida (Carthy 1994, Blair et al. 2000, Herren and Ehrhart 2000, Rumbold et al. 2001, Florida Fish and Wildlife Conservation Commission 2002), so responses of green turtles to beach restoration are largely unknown. Green turtles exhibit strong nest site fidelity (Meylan et al. 1990, Allard et al. 1994) and typically nest in or near dunes (Witherington 1986, Brock 2005), making them especially sensitive to dune restoration projects. I report here the effects of dune restoration on abiotic properties of the nesting beach and consequent effects on green turtle reproduction. I focused on hatching success because it measures how many eggs successfully developed (Limpus et al. 1979). I compared

abiotic characteristics within green turtle nests in natural and engineered dunes to determine if dune restoration altered the microenvironment of nests. I tested to determine if differences in date nest was laid, mean sand grain size, percent porosity, percent moisture, pH, nest temperature, and percent calcium carbonate affected green turtle hatching success. Results of my study will determine whether emergency use of fill material from inland sources provides an adequate environment for the proper development of green turtle eggs.

CHAPTER TWO: METHODS

Study System

Green turtles are distributed throughout the major oceans (Bowen et al. 1992) and Florida populations are listed as endangered under the Endangered Species Act of 1973 (National Marine Fisheries Service and U.S. Fish and Wildlife Service 1991). Individual female green turtles nest biennially and deposit an average of four clutches per season in sandy beaches (Johnson 1994, Johnson and Ehrhart 1996). Green turtles nest from late May through late September (Johnson and Ehrhart 1996) with an average clutch size of 126 eggs (Ehrhart unpub. Data), and nests laid at ACNWR account for more than 1/3rd of all green turtle nests in the USA (Meylan et al. 1995).

I conducted this study during the 2006 marine turtle nesting season at the ACNWR in southern Brevard County, on Florida's east-central coast (Figure 1). After several destructive hurricane seasons, engineered dunes were constructed along privately - owned properties within the refuge to replace sand lost to erosion. Engineered dunes comprised 76% of ACNWR, leaving approximately 24% with natural dune along undeveloped beachfront. The study area included sections of engineered dunes placed in Spring 2005, and remaining natural areas. I did not include beach tracts that underwent further construction in Spring 2006.

Four sources of replacement sand were used in dune restoration (Figure 2). Most fill material (estimated 72%) was from a quarry in Rockledge, FL, approximately 51 km from ACNWR. The remainder came from Oak Hill (15%), Astatula (5%), and Indian River County (8%), FL (McGarry 2007). These quarries are located on ancient dunes formed during previous periods of high sea levels. Dunes located in Astatula were formed during the Miocene period

and are comprised of clay and sand. The remaining quarries are located on dunes that were formed during the Holocene beginning 10,000 years ago (Allen and Main 2005). The age of sand in Titusville, Florida, located along the coast at approximately the same longitude as the remaining three quarries, was formed approximately 8,070 years ago (Rink and Forrest 2005). Exactly where fill material from the five quarries was used to create new dunes is unknown.

Field Work

Between 30 June and 21 August 2006, I surveyed the beach at night looking for nesting females on natural and engineered dunes (Figure 3). After the female deposited her eggs and returned to the ocean, I excavated the nest to locate eggs. I measured nest depth from the eggs to the sand surface, carefully removed the eggs, and measured the distance from the sand surface to the bottom of the egg chamber. I removed 150 mL core of sand from the center of the southern egg chamber wall for later laboratory analysis. Sand samples were sealed in plastic storage bags and frozen until analysis. I returned eggs to the egg chamber in the same order they were removed, with the exception that I included a temperature data logger (Hobo H8, (Onset Computer Corporation 2002) after half of the eggs were replaced. Data loggers recorded incubation temperatures hourly. I placed small wooden stakes in line westward of the clutch to relocate it. I monitored nests throughout incubation for signs of disturbance and ultimately hatchling emergence. When signs of emergence were detected, I recorded nest location and date of emergence. Hatchlings often leave the nest over the course of several nights, therefore I waited at least 72 h to allow any viable hatchlings to emerge. After this period, I returned and inventoried egg remains, recording the number of hatched and undeveloped eggs in each clutch. Hatched eggs were identified by their dry clean appearance. Whole eggs were categorized as

addled, embryo, fetus, or infertile (Osegovic 2001). I recorded gross embryonic development as presented by Miller (1985) and noted if eggs were depredated by ghost crabs or destroyed by plant roots.

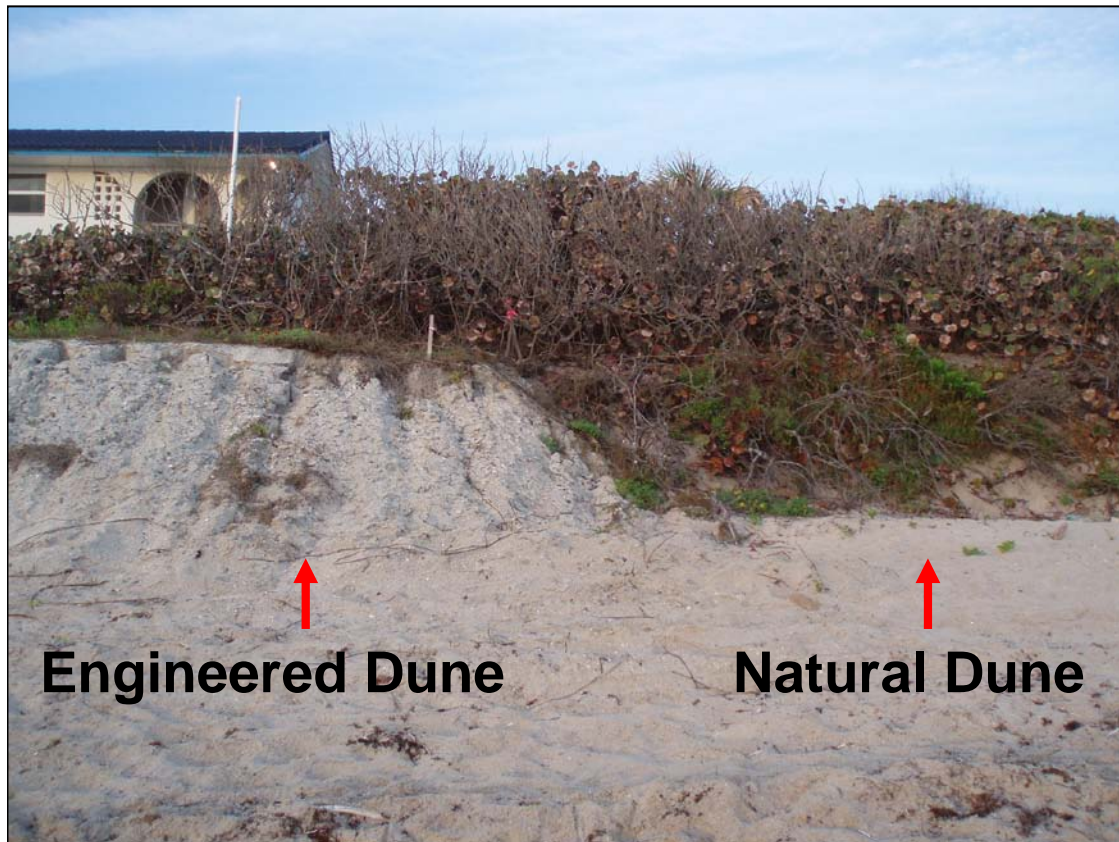


Figure 3. Typical natural dune and engineered dune within Archie Carr National Wildlife Refuge, FL, USA, following dune construction in 2005.

I marked and sampled 19 nests in natural dunes and 20 nests in engineered dunes. Four nests were depredated by raccoons (three engineered and one natural) prior to study completion and were excluded from analyses.

Laboratory analyses

Sand samples were returned to the laboratory where I measured six abiotic characteristics: mean grain size, percent calcium carbonate, percent sand moisture, sand color, percent porosity and pH. These six factors, in addition to nest depth and temperature, were used to determine if engineered dune substrate differed from natural sand.

I determined sand grain size distribution using standard testing sieves of varying mesh sizes (Mortimer 1990). I weighed each sand sample, then placed it into seven stacked U.S. Standard 8" (20.3 cm) testing sieves (mesh sizes of 2.0, 1.0, 0.5, 0.25, 0.125, 0.088, and 0.062 mm), which were shaken for 10 min. in a Ro Tap machine (Mentor, Ohio). I weighed the sand remaining in each sieve then calculated percent mass of each grain size using the initial, dried total mass. I analyzed grain size using GRADISTAT software (Blott and Pye 2001) which is based on the Folk and Ward method (1957). I used geometric means instead of arithmetic means to account for non-normal distributions of grain sizes (Blott and Pye 2001).

I determined percent calcium carbonate content using the gravimetric method outlined by Loeppert and Suarez (1996). I transferred a known weight of sand (approximately 1 g) to a previously weighed Erlenmeyer flask and stopper that contained 10 mL of 3 M HCl. Carbonates reacted with the acid to produce carbon dioxide. Flasks were continuously vented and weighed until they reached constant mass. I determined the amount of CO₂ lost as the difference between initial and final flask weights. I used total mass of CO₂ lost to determine the calcium carbonate content, as follows:

$$\text{CaCO}_3 \% = [(\text{CO}_2 \text{ lost/g soil}) (\text{g CaCO}_3 \text{ mol}^{-1} / \text{g CO}_2 \text{ mol}^{-1})] (100) =$$
$$(\text{g CO}_2 \text{ lost/ g soil}) (2.273) (100)$$

I determined percent moisture content using sand samples collected at time of egg deposition. Initial mass was taken before placing sand into a drying oven. I dried samples at 40° C for 24 h then reweighed them, and calculated percent moisture content as [(mass of moist soil – mass of dry soil)/ mass of dry soil] x 100 (Bowles 1992).

I determined sand color using Munsell Soil Color Charts (1988). I recorded hue, value, and chroma for a small sub-sample of sand. I repeated this process with the same sample after wetting it with water.

Porosity characterizes sand structure and is defined as the proportion of air-filled space in a soil sample (Carter and Ball 1993). I calculated total porosity from the 150 mL sand sample collected from the egg chamber wall at the middle of the clutch. I calculated total porosity as $\text{total porosity (\%)} = 100(1 - (\text{Bulk density}/2.65))$, where bulk density equals the weight of the sample divided by the volume of the sample container (g / mL) and 2.65 Mg m⁻³ is the soil particle density of mineral soil (Carter and Ball 1993).

I determined pH using methods outlined in the Florida Method of Test for Determining pH of Soil and Water (Florida Department of Transportation 2000).

I used hatching success of nests as a measure of their reproductive success. Hatching Success = total eggs hatched / total clutch size.

To determine if the two dune types differed in physical characteristics, I used Multivariate Analysis of Variance (MANOVA) to compare the mean vector of the eight abiotic characteristics of the natural and engineered dune areas. To meet the criteria of a normal distribution and homogenous variances, I transformed porosity data using the reciprocal square transformation and calcium carbonate, mean grain size and initial moisture using the square root

transformation. Levene's test for equality of error variances was significant for calcium carbonate and mean grain size, violating the assumption of equal variances. I used a nonparametric test (Kruskal – Wallis) to confirm the results of the MANOVA due to violation of assumptions. I used MANOVA to determine if the percentage in the five main categories of sand, as determined from the Folk and Ward method of sand categorization, differed significantly. I used a nonparametric test (Kruskal – Wallis) to check the results of the MANOVA due to violation of equal variance assumptions. I used a Chi-square test to determine if sand colors differed between natural and engineered dunes.

I compared mean hatching success between the dune types using Analysis of Variance (ANOVA). I used backward stepwise regression to determine which variables produced a regression model that best explained variation in hatching success, by removing independent variables that were not strong predictors. I used MANOVA to determine differences in the developmental stages in which eggs ceased being viable (addled, fetus and embryo) as well as those affected by ghost crabs (*Ocypode quadrata*) and plant roots. Comparisons were considered significantly different at $\alpha = 0.05$ unless otherwise noted.

I marked my study nests in four, week-long periods during the height of the green turtle nesting season. I selected 10 nests per week, 5 in each dune type. I choose study nests using a haphazard methodology due to the unpredictability in nest placement. As I traversed the length of the study area at night, I marked nests as I found them if they were deposited in either engineered or natural dune. In order for a nest to be considered in engineered dune, it needed to be on the dune face and the egg chamber needed to be made of only fill material. Nests containing any visible layer of natural sand were not included in this study. As a result of the

haphazard nest marking scheme, I analyzed the data for any spatial or temporal autocorrelations. I found no temporal correlations (Durbin – Watson = 2.644). After analyzing data using the software program SAM 4.0 (Rangel et al. 2010), three pairs of nests showed spatial autocorrelation ($p < 0.05$). However, the results of the linear regression in SAM 4.0, which included the spatial data, date, and mean grain size, did not differ from the backward stepwise regression performed in SPSS ($F = 4.892$, $r^2 = 0.259$, $p = 0.015$) indicating spatial correlation did not affect the findings of this study.

This study was permitted by the Florida Fish and Wildlife Conservation Commission on Marine Turtle Permit # 025 under principal investigator Dr. Llewellyn Ehrhart. This work was also approved by the University of Central Florida's Institutional Animal Care and Use Committee.

CHAPTER THREE: RESULTS

Abiotic Characteristics

All nest substrate samples were sand and none contained gravel, silt or clay (Figure 4). Sand characteristics (Tables 1 and 2) differed significantly between dune types (Pillai's Trace, $p = 0.576$; $F_{8,22} = 3.735$, $p < 0.007$). Due to MANOVA requiring equal sample sizes, four nests (one natural and three engineered) with missing values were excluded from the analysis as indicated by ND in Table 2, resulting in comparison of 17 natural and 14 engineered nests. Results herein are reported as means \pm one standard error.

Table 1. Univariate results for abiotic sand characteristics in natural ($n = 17$) and engineered dunes ($n = 14$) within Archie Carr National Wildlife Refuge, FL, USA.

Dependent Variable	$F_{1,29}$	p	Dune Type	95% Confidence Interval	
				Lower Bound	Upper Bound
Grain Size (μm)	25.999	0.0001	Natural	397.7	457.4
			Engineered	211.7	337.6
Calcium Carbonate (%)	13.736	0.001	Natural	24.0	30.0
			Engineered	6.8	23.4
Moisture (%)	14.000	0.001	Natural	2.8	3.8
			Engineered	4.1	5.1
Porosity (%)	0.011	0.917	Natural	39.8	43.5
			Engineered	39.8	43.0
pH	0.687	0.414	Natural	7.7	7.8
			Engineered	7.6	7.8
Top Depth (cm)	1.793	0.191	Natural	58.2	67.9
			Engineered	51.0	64.8
Bottom Depth (cm)	1.256	0.272	Natural	85.1	92.0
			Engineered	77.9	91.6
Mean Temperature ($^{\circ}\text{C}$)	0.003	0.96	Natural	30.6	31.4
			Engineered	30.7	31.2

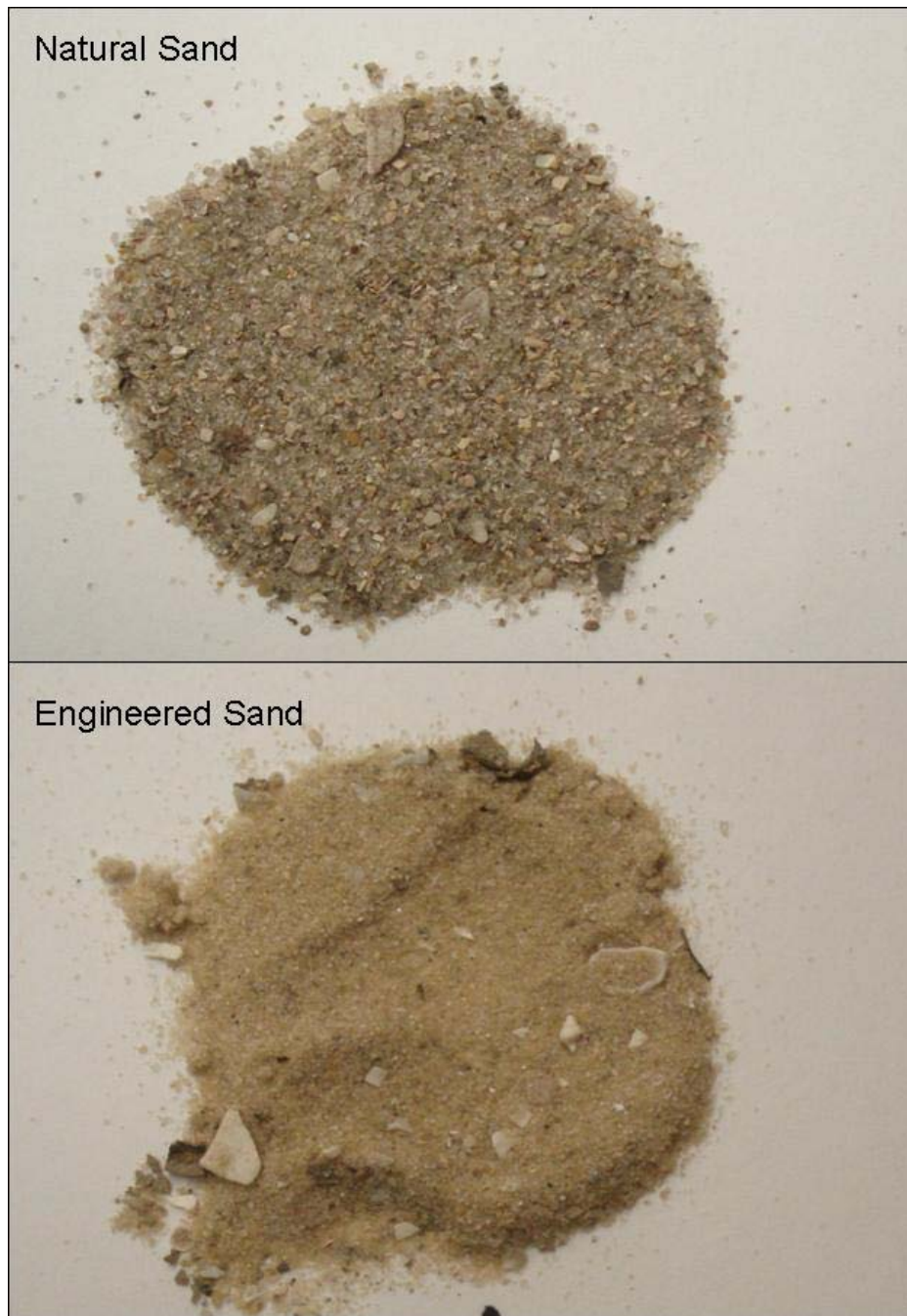


Figure 4. Examples of natural and engineered sand collected in 2006 from Archie Carr National Wildlife Refuge, FL, USA.

Table 2. Values for the abiotic characteristics for engineered and natural dunes within Archie Carr National Wildlife Refuge, FL USA. ND indicates no data.

Nest ID No.	Dune type	Date	Porosity (%)	Moisture (%)	Depth (cm)	pH	CaCO ₃ (%)	Temperature (C°)	Grain Size (µm)
B06/123	Natural	30-Jun-06	42.90	2.93	89.00	7.57	25.63	31.40	390.86
B06/137	Natural	30-Jun-06	41.78	2.32	89.00	7.73	33.04	31.85	485.84
B06/157	Natural	7-Jul-06	48.17	3.34	80.00	7.78	25.78	31.21	387.26
B06/160	Natural	8-Jul-06	37.51	ND	86.00	7.54	43.04	30.77	484.15
B06/166	Natural	8-Jul-06	40.41	3.81	97.00	7.93	32.14	31.73	509.09
B06/182	Natural	16-Jul-06	38.36	4.96	79.00	7.98	17.49	31.42	325.12
B06/183	Natural	18-Jul-06	38.14	3.05	87.00	7.71	35.81	31.65	508.81
B06/244	Natural	20-Jul-06	39.37	2.82	100.50	7.85	26.41	30.83	430.57
B06/211	Natural	22-Jul-06	43.09	2.50	86.00	7.94	34.96	31.24	512.74
B06/228	Natural	25-Jul-06	41.52	2.89	78.00	7.60	24.69	31.28	427.21
B06/229	Natural	26-Jul-06	38.48	3.20	93.00	7.48	24.21	30.24	402.02
B06/232	Natural	26-Jul-06	41.13	1.87	98.00	7.77	25.24	31.23	402.94
B06/241	Natural	28-Jul-06	51.87	2.69	93.00	7.66	29.05	31.69	443.89
B06/230	Natural	29-Jul-06	43.05	3.84	85.00	7.41	26.26	30.99	463.04
B06/299	Natural	19-Aug-06	38.47	2.91	94.00	8.03	23.44	30.42	345.88
B06/300	Natural	20-Aug-06	41.94	3.43	90.00	7.81	14.23	29.35	358.26
B06/301	Natural	20-Aug-06	40.60	2.98	84.00	7.74	26.15	30.47	404.82
B06/302	Natural	21-Aug-06	38.72	6.44	83.00	7.73	34.22	30.17	469.83
B06/138	Engineered	6-Jul-06	48.07	5.94	82.00	7.55	9.03	31.47	266.57
B06/155	Engineered	6-Jul-06	47.80	4.97	ND	7.60	7.03	31.52	262.19
B06/159	Engineered	7-Jul-06	ND	5.27	75.00	7.56	17.45	31.02	235.88
B06/156	Engineered	7-Jul-06	39.51	5.50	96.00	7.62	24.83	31.15	297.22
B06/165	Engineered	8-Jul-06	38.13	5.09	83.00	7.89	14.06	31.49	311.19
B06/195	Engineered	18-Jul-06	40.44	5.37	89.00	7.71	9.70	31.80	168.93
B06/220	Engineered	23-Jul-06	39.66	5.75	79.00	7.70	1.67	31.37	259.99
B06/225	Engineered	23-Jul-06	42.67	4.17	110.00	7.74	27.11	30.98	392.28
B06/227	Engineered	25-Jul-06	41.40	4.39	63.00	7.23	1.94	30.89	162.54
B06/204	Engineered	28-Jul-06	43.98	3.45	80.00	7.68	19.74	30.70	295.74
B06/239	Engineered	28-Jul-06	47.81	5.37	75.00	7.48	8.13	ND	197.93
B06/240	Engineered	28-Jul-06	44.80	2.71	79.00	7.78	28.02	30.95	425.80
B06/289	Engineered	18-Aug-06	39.48	4.16	83.00	8.14	4.41	30.38	198.26
B06/291	Engineered	18-Aug-06	40.40	4.06	73.00	7.62	7.11	30.45	189.30
B06/292	Engineered	19-Aug-06	40.69	4.79	91.00	7.73	4.63	30.80	163.97
B06/310	Engineered	21-Aug-06	38.47	3.92	100.00	7.81	53.04	31.10	519.21
B06/311	Engineered	21-Aug-06	41.66	4.97	79.00	7.49	5.97	30.46	194.28

Mean sand grain size in natural dunes was 427.5 ± 14.1 µm versus 274.6 ± 29.1 µm in engineered dunes (Figure 5). Sand categories differed significantly between dune types (Pillai's Trace, $p = 0.596$; $F_{5,28} = 8.254$, $p = 0.0001$; Table 3, Figures 5, 6). Natural dune contained more coarse sand ($25.8\% \pm 2.5$ vs $12.2\% \pm 1.9$; Table 4) and medium sand than engineered dune ($62.5\% \pm 2.1$ vs $36.0\% \pm 4.5$) but less fine ($4.2\% \pm 0.81$ vs $28.5\% \pm 3.9$) and very fine sand (2.7

% \pm 0.5 vs. 18.7 % \pm 2.6; Figure 6). The percentage of very coarse sand between dune types did not differ significantly (4.7% \pm 0.8 vs. 4.5% \pm 0.9). Error variances were not equal for the medium, fine and very fine grain sizes. Due to the violation of assumptions in MANOVA, I checked the results using Kruskal - Wallis tests (all $\chi^2 > 14.75$, $p < 0.0001$), which confirmed MANOVA results.

Table 3. Univariate results for five sand categories (very coarse, coarse, medium, fine and very fine) in natural and engineered dunes within Archie Carr National Wildlife Refuge, FL, USA.

Sand Category	F _{1,32}	p	Dune Type	95% Confidence Interval	
				Lower Bound	Upper Bound
Very Coarse (%)	0.026	0.874	Natural	2.95	6.53
			Engineered	2.52	6.56
Coarse (%)	18.228	0.0001	Natural	20.44	31.26
			Engineered	8.17	16.29
Medium (%)	27.745	0.0001	Natural	57.99	67.10
			Engineered	26.33	45.66
Fine (%)	36.546	0.0001	Natural	2.43	5.88
			Engineered	20.14	36.87
Very Fine (%)	36.828	0.0001	Natural	1.58	3.81
			Engineered	13.21	24.15

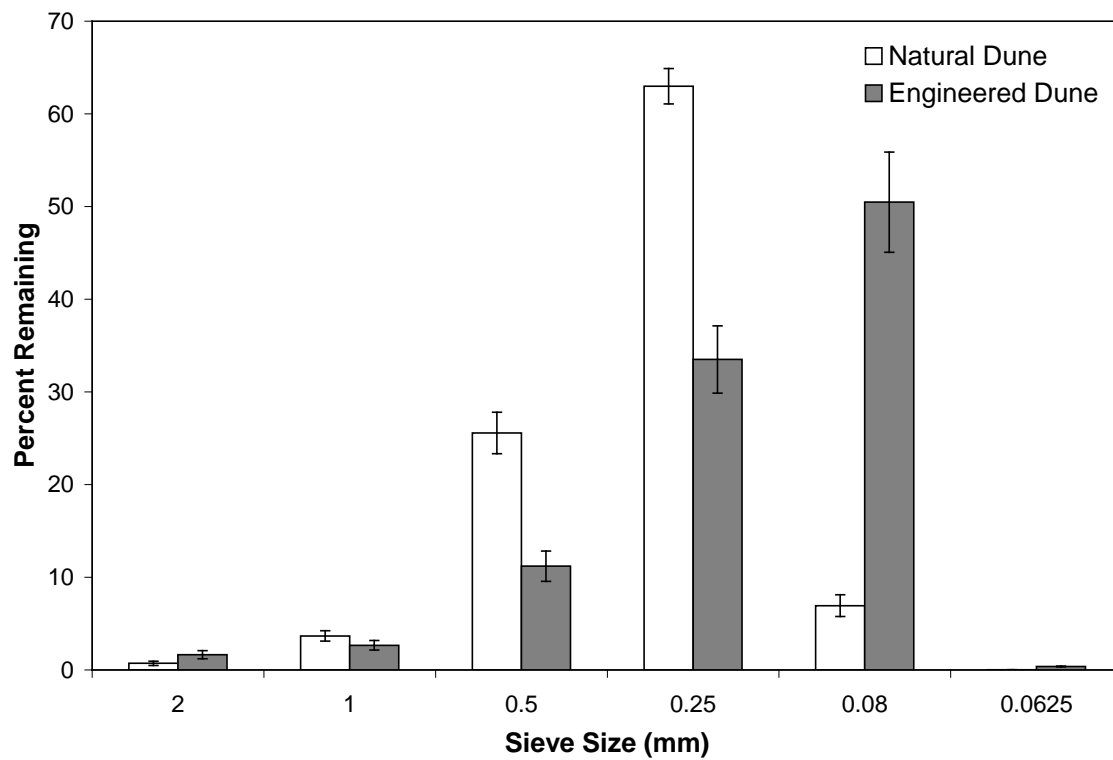


Figure 5. Sand composition from natural and engineered dunes within Archie Carr National Wildlife Refuge, FL, USA. Mean bars (± 1 SE) are percentage of sand remaining in each 20.3 cm diameter testing sieve.

Table 4. Folk and Ward (1966) sand categories (%), sorting, skewness, kurtosis in natural and engineered dunes within Archie Carr National Wildlife Refuge, FL, USA.

Nest ID No.	Dune type	Date	Very coarse	Coarse	Medium	Fine	Very fine	Sorting	Skewness	Kurtosis
B06/123	Natural	30-Jun-06	1.47	18.49	73.52	3.96	2.56	1.52	0.13	1.32
B06/137	Natural	30-Jun-06	5.08	40.30	50.67	2.38	1.56	1.60	0.11	0.75
B06/157	Natural	7-Jul-06	2.40	18.28	68.02	6.87	4.43	1.64	0.04	1.55
B06/160	Natural	8-Jul-06	12.27	26.66	56.17	2.97	1.92	1.81	0.36	1.03
B06/166	Natural	8-Jul-06	10.24	37.19	50.99	0.94	0.61	1.72	0.23	0.93
B06/182	Natural	16-Jul-06	0.39	8.64	72.71	11.10	7.16	1.60	-0.19	1.59
B06/183	Natural	18-Jul-06	9.13	39.01	50.38	0.89	0.58	1.69	0.20	0.89
B06/244	Natural	20-Jul-06	2.48	27.02	65.43	3.08	1.99	1.54	0.24	0.92
B06/211	Natural	22-Jul-06	6.47	44.64	46.81	1.25	0.82	1.63	0.07	0.82
B06/228	Natural	25-Jul-06	2.22	27.90	62.14	4.70	3.04	1.65	0.09	1.12
B06/229	Natural	26-Jul-06	3.57	18.85	69.43	4.94	3.20	1.62	0.12	1.46
B06/232	Natural	26-Jul-06	5.69	18.78	61.42	8.55	5.54	1.80	0.10	1.63
B06/241	Natural	28-Jul-06	4.56	26.42	66.54	1.50	0.97	1.55	0.28	0.90
B06/230	Natural	29-Jul-06	5.80	30.22	62.27	1.03	0.67	1.60	0.27	0.87
B06/299	Natural	19-Aug-06	0.50	10.82	72.76	9.68	6.24	1.56	-0.09	1.62
B06/300	Natural	20-Aug-06	1.59	13.19	73.24	7.16	4.72	1.56	-0.05	1.63
B06/301	Natural	20-Aug-06	1.27	21.11	73.39	2.57	1.66	1.47	0.26	1.09
B06/302	Natural	21-Aug-06	6.94	30.46	60.90	1.03	0.67	1.64	0.29	0.90
B06/138	Engineered	6-Jul-06	2.44	11.28	49.44	22.12	14.61	1.95	-0.17	1.01
B06/155	Engineered	6-Jul-06	5.92	10.10	43.23	24.50	16.16	2.11	-0.05	1.08
B06/159	Engineered	7-Jul-06	4.68	13.04	25.66	34.15	22.43	2.16	0.19	0.87
B06/156	Engineered	7-Jul-06	4.35	20.91	35.05	23.97	15.70	2.18	-0.04	0.86
B06/165	Engineered	8-Jul-06	4.01	14.93	54.12	16.23	10.67	1.95	-0.13	1.34
B06/195	Engineered	18-Jul-06	3.00	3.37	13.02	48.65	31.88	1.80	0.25	1.18
B06/220	Engineered	23-Jul-06	2.43	10.59	47.54	23.70	15.66	1.96	-0.15	0.97
B06/225	Engineered	23-Jul-06	3.45	21.40	58.79	9.90	6.44	1.78	0.02	1.48
B06/227	Engineered	25-Jul-06	0.61	3.04	14.13	49.49	32.64	1.67	0.16	1.00
B06/204	Engineered	28-Jul-06	6.37	17.06	36.96	23.84	15.68	2.27	0.02	0.99
B06/239	Engineered	28-Jul-06	2.74	6.78	22.01	41.33	27.07	1.97	0.24	0.97
B06/240	Engineered	28-Jul-06	4.97	24.32	60.74	6.03	3.92	1.73	0.09	1.25
B06/289	Engineered	18-Aug-06	8.18	4.04	16.64	42.95	28.12	2.23	0.37	1.34
B06/291	Engineered	18-Aug-06	1.82	5.61	20.75	43.35	28.40	1.89	0.23	0.99
B06/292	Engineered	19-Aug-06	1.06	2.30	14.70	49.79	32.14	1.66	0.16	0.99
B06/310	Engineered	21-Aug-06	17.67	25.57	48.12	5.23	3.41	2.03	0.20	1.03
B06/311	Engineered	21-Aug-06	4.41	6.32	26.98	37.58	24.63	1.96	0.27	1.01

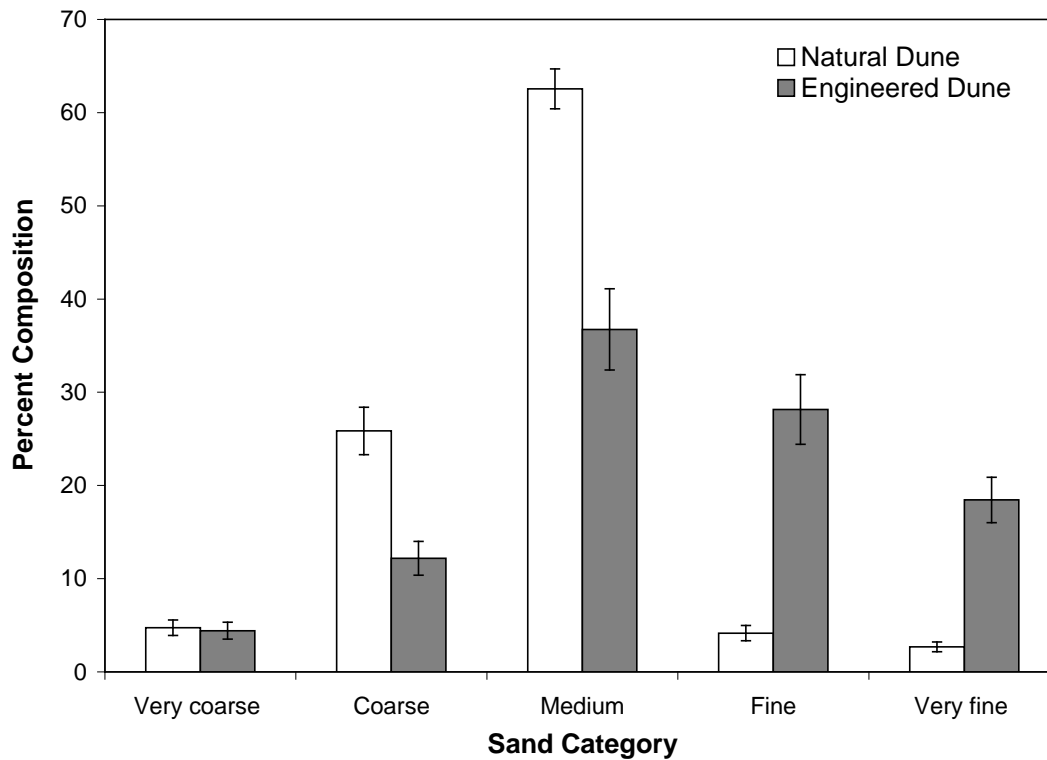


Figure 6. Natural and engineered dunes within Archie Carr National Wildlife Refuge, Florida, USA, differed in sand composition. Bars are mean (\pm SE) as determined with the Folk and Ward (1966) categorization.

Natural dune contained a significantly higher mean percentage of calcium carbonate (27.0 ± 1.4 % vs. 15.1 ± 3.8 %) but less mean moisture (3.29 ± 0.26 % vs. 4.59 ± 0.25 %) than engineered dune. Dry sand colors differed significantly (Likelihood ratio = 20.97, d. f. = 2, $p = 0.001$, Table 5). Natural dune sand was mostly white ($n = 16$) and some gray ($n = 4$), while engineered dunes were mostly very pale brown ($n = 12$) or white ($n = 8$; Figure 7). However, porosity, pH, nest depth and temperature did not differ significantly between dune types (all $F < 1.31$, $p > 0.05$). Mean porosity (41.6 ± 0.93 % versus 41.5 ± 0.68 %), and sand pH (7.75 ± 0.04 versus 7.68 ± 0.05), and nest depth to the top (63.05 ± 2.4 cm vs. 57.9 ± 3.2 cm) and bottom of

the egg chamber (88.5 ± 1.7 vs. 85.1 ± 2.9 cm) were all similar in natural dune and engineered dunes. Overall daily mean temperature in natural dune and engineered dunes also was similar: 31.0 ± 0.16 °C versus 31.0 ± 0.10 °C, respectively.

Table 5. Munsell Color (1991) values for hue, value/chroma and color name for sands sampled on natural and engineered dunes within Archie Carr National Wildlife Refuge FL, USA, when dry and moist.

Nest ID No.	Dune type	Dry			Moist		
		Hue	Value/ Chroma	Name	Hue	Value/ Chroma	Name
B06/123	Natural	10YR	8/2	white	10YR	7/3	very pale brown
B06/137	Natural	10YR	8/2	white	10YR	7/4	very pale brown
B06/157	Natural	10YR	8/1	white	10YR	6/3	pale brown
B06/160	Natural	10YR	8/1	white	10YR	7/3	very pale brown
B06/166	Natural	10YR	8/1	white	10YR	7/3	very pale brown
B06/182	Natural	10YR	8/1	white	10YR	5/3	brown
B06/183	Natural	10YR	8/2	white	10YR	7/3	very pale brown
B06/244	Natural	10YR	8/2	white	10YR	7/3	very pale brown
B06/211	Natural	10YR	8/1	white	10YR	7/3	very pale brown
B06/228	Natural	10YR	8/1	white	10YR	7/3	very pale brown
B06/229	Natural	10YR	7/2	light gray	10YR	6/3	pale brown
B06/232	Natural	10YR	8/2	white	10YR	6/3	pale brown
B06/238	Natural	10YR	8/2	white	10YR	6/3	pale brown
B06/241	Natural	10YR	8/2	white	10YR	7/3	very pale brown
B06/230	Natural	10YR	8/1	white	10YR	7/3	very pale brown
B06/290	Natural	10YR	7/1	light gray	10YR	5/2	grayish brown
B06/299	Natural	10YR	7/1	light gray	10YR	5/1	gray
B06/300	Natural	10YR	7/2	light gray	10YR	6/3	pale brown
B06/301	Natural	10YR	8/2	white	10YR	7/3	very pale brown
B06/302	Natural	10YR	8/2	white	10YR	7/3	very pale brown
B06/138	Engineered	10YR	8/2	white	10YR	7/3	very pale brown
B06/155	Engineered	10YR	8/2	white	10YR	7/3	very pale brown
B06/156	Engineered	10YR	7/3	very pale brown	10YR	6/3	pale brown
B06/159	Engineered	10YR	8/4	very pale brown	10YR	7/4	very pale brown
B06/165	Engineered	10YR	8/2	white	10YR	7/4	very pale brown
B06/195	Engineered	10YR	7/4	very pale brown	10YR	6/4	light yellowish brown
B06/209	Engineered	10YR	7/3	very pale brown	10YR	5/3	brown
B06/220	Engineered	10YR	8/2	white	10YR	7/4	very pale brown
B06/221	Engineered	10YR	8/2	white	10YR	6/3	pale brown
B06/225	Engineered	10YR	8/1	white	10YR	6/3	pale brown
B06/226	Engineered	10YR	7/3	very pale brown	10YR	5/3	brown
B06/227	Engineered	10YR	7/3	very pale brown	10YR	6/4	light yellowish brown
B06/204	Engineered	10YR	8/3	very pale brown	10YR	6/4	light yellowish brown
B06/239	Engineered	10YR	7/4	very pale brown	10YR	6/4	light yellowish brown
B06/240	Engineered	10YR	8/1	white	10YR	7/4	very pale brown
B06/289	Engineered	10YR	7/3	very pale brown	10YR	6/3	pale brown
B06/291	Engineered	10YR	7/4	very pale brown	10YR	6/4	light yellowish brown
B06/292	Engineered	10YR	7/4	very pale brown	10YR	6/5	brownish yellow
B06/310	Engineered	10YR	8/2	white	10YR	7/4	very pale brown
B06/311	Engineered	10YR	7/3	very pale brown	10YR	5/3	brown

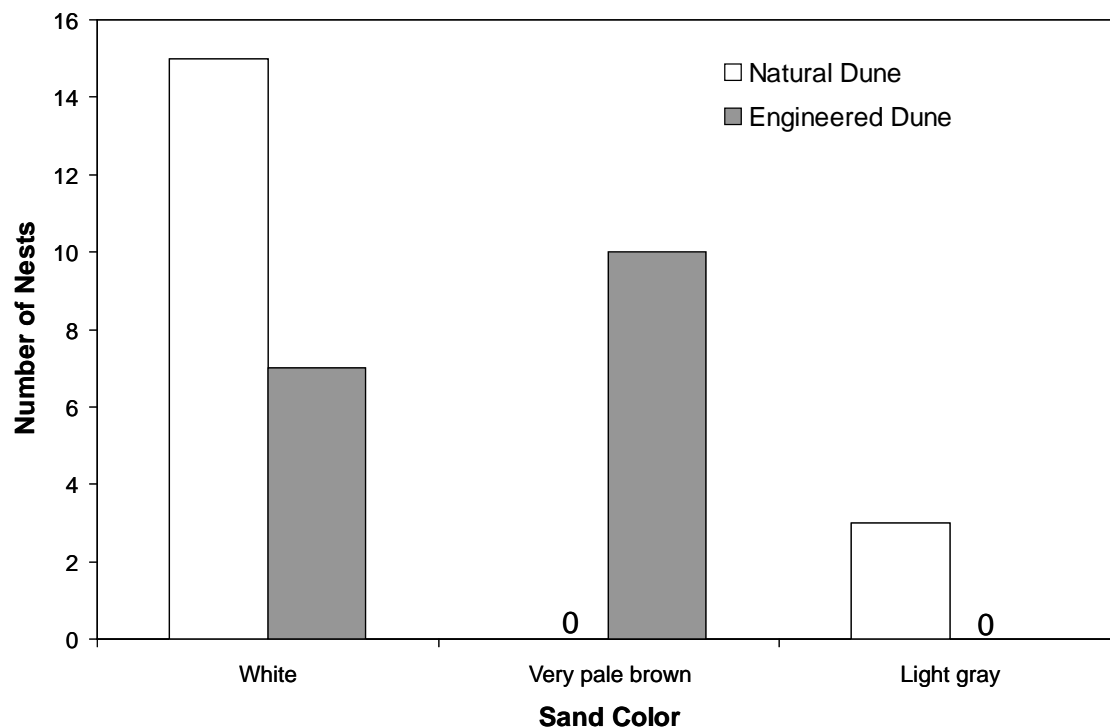


Figure 7. Distribution of sand color on natural and engineered dunes within Archie Carr National Wildlife Refuge, Florida, USA. Sand color differed significantly between dune type (Chi-square likelihood ratio = 20.97, d. f. = 2, $p = 0.001$), with natural dune having mostly white sand and engineered dune having predominately very pale brown sand. Colors based on Munsell color charts (Munsell Color 1988).

Hatching Success

Number of eggs per nest ranged from 91 - 185 in natural and 105 - 201 in engineered dunes (Table 6). Hatching success was significantly higher in natural dune compared to engineered dune ($65.8\% \pm 5.3$ vs. $44.7\% \pm 6.2$, $F_{1,33} = 6.628$, $p = 0.015$). Mean number of hatchlings remaining in nests was similar in natural and engineered dunes ($1.58\% \pm 0.40$ vs. $1.39\% \pm 0.31$; $t = -0.356$, d.f. = 33, $p = 0.724$). The percentage of addled eggs was significantly higher in engineered dunes (34.71% vs. 20.28% , d.f. = 33, $F = 5.085$, $p = 0.031$) and the

percentage of eggs affected by ghost crabs was close to being statistically higher in the engineered dune (17.59% vs. 13.09%, d. f. = 33, $F = 3.402$, $p = 0.074$).

The total number of green turtle nests laid in ACNWR in 2006 was 1,383 with an average clutch size of 135 eggs. A total of 57% of these were laid in engineered dunes which had 21% fewer hatched eggs than natural nests, resulting in an estimated loss of 22, 646 eggs.

Backward stepwise regression revealed that date nest was laid and mean grain size were the variables in the reduced model that explained the most variation in hatching success; hatching success decreased as the season progressed and with finer sands (hatching success = $0.211 + (-0.005)(\text{date}) + (0.026)(\text{mean grain size in } \mu\text{m})$; $R^2 = 0.259$, $F_{2, 28} = 4.889$, $p = 0.015$). Calcium carbonate was collinear with grain size and was removed from the initial backward stepwise regression model.

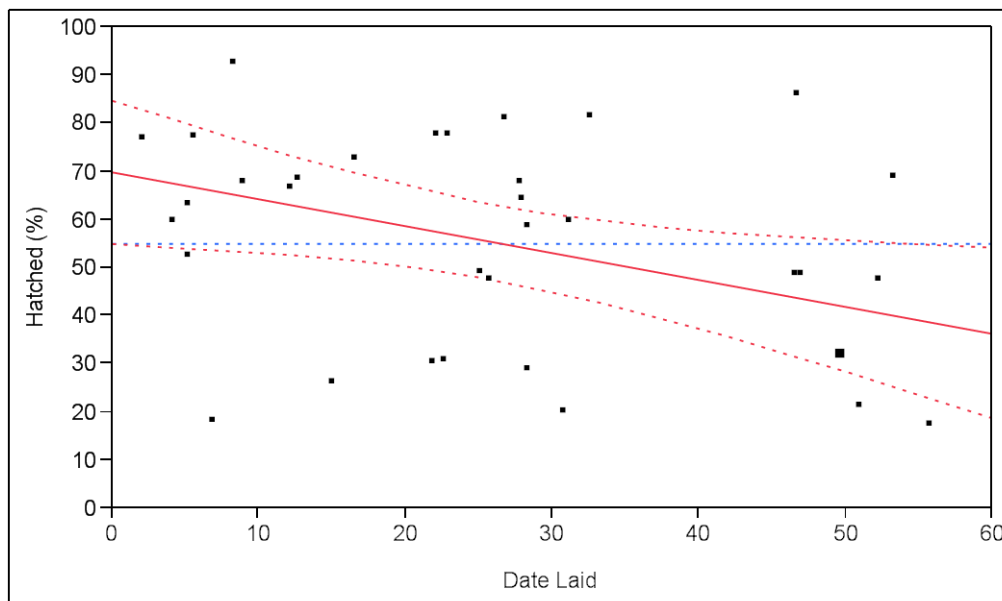


Figure 8. Leverage plot of green turtle hatching success (%) versus date nest was laid in Archie Carr National Wildlife Refuge, Florida, USA. The solid red line is the regression line, the dashed blue line is the average hatching success and the red dashed line represents the region of 95% confidence intervals.

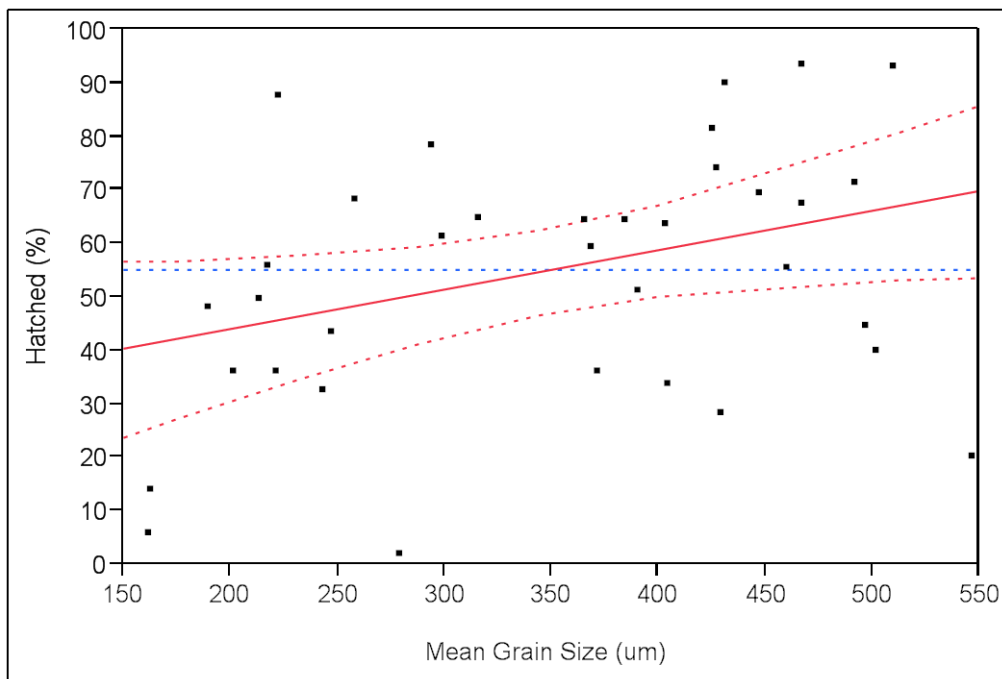


Figure 9. Leverage plot of green turtle hatching success (%) versus mean sand grain size in Archie Carr National Wildlife Refuge, Florida, USA. The solid red line is the regression line, the dashed blue line is the average hatching success and the red dashed line represents the region of 95% confidence intervals.

Table 6. Table summarizing status of green turtle eggs at the end of the incubation period in engineered and natural nests within Archie Carr National Wildlife Refuge, FL, USA.

Nest ID	Dune Type	Date	Total Number of Eggs	Hatched (%)	Hatchlings Remaining (%)	Addled (%)	Embryo (%)	Fetus (%)	Ghost Crab (%)	Plant Roots (%)
B06/123	Natural	30-Jun-2006	108	81.48	5.56	12.06	0.00	6.49	0.00	0.00
B06/137	Natural	30-Jun-2006	124	72.73	3.41	33.11	1.62	3.23	0.00	0.00
B06/157	Natural	7-Jul-2006	104	72.27	0.84	7.71	0.96	20.23	0.84	0.00
B06/160	Natural	8-Jul-2006	110	79.58	0.70	23.62	0.00	2.73	0.00	0.00
B06/166	Natural	8-Jul-2006	105	83.48	2.61	3.81	0.00	13.35	0.00	0.00
B06/182	Natural	16-Jul-2006	102	71.88	0.78	12.70	5.86	9.77	5.47	0.00
B06/183	Natural	18-Jul-2006	107	45.80	0.00	26.24	2.81	16.87	5.34	11.45
B06/244	Natural	20-Jul-2006	100	86.01	0.00	11.01	0.00	2.00	4.90	0.00
B06/211	Natural	22-Jul-2006	100	96.43	0.00	2.99	0.00	0.00	0.00	0.00
B06/228	Natural	25-Jul-2006	96	75.57	0.76	7.29	0.00	12.49	9.92	0.00
B06/229	Natural	26-Jul-2006	99	64.41	0.00	19.18	1.01	14.13	6.78	0.00
B06/232	Natural	26-Jul-2006	97	34.59	1.62	54.54	3.09	3.09	31.89	1.62
B06/241	Natural	28-Jul-2006	90	69.01	0.00	7.82	1.12	2.23	14.08	9.86
B06/230	Natural	29-Jul-2006	100	92.39	1.09	2.99	1.00	1.99	1.09	0.00
B06/299	Natural	19-Aug-2006	59	21.98	5.49	34.11	6.82	11.94	43.96	0.00
B06/300	Natural	20-Aug-2006	110	49.31	2.78	32.86	14.61	4.56	9.72	0.00
B06/301	Natural	20-Aug-2006	98	75.00	0.78	14.36	1.03	6.15	8.59	0.00
B06/302	Natural	21-Aug-2006	86	29.00	2.00	57.96	3.48	2.32	16.00	0.00
B06/138	Engineered	6-Jul-2006	116	57.04	3.52	33.59	0.00	13.78	4.23	0.00
B06/155	Engineered	6-Jul-2006	130	45.98	2.30	39.32	4.63	18.50	7.47	0.00
B06/159	Engineered	7-Jul-2006	118	68.83	0.00	35.74	0.00	5.11	0.00	0.00
B06/156	Engineered	7-Jul-2006	105	14.95	2.80	34.20	5.70	7.60	0.00	37.38
B06/165	Engineered	8-Jul-2006	105	90.58	0.72	11.41	0.00	0.95	0.00	0.00
B06/195	Engineered	18-Jul-2006	134	11.94	0.00	32.77	2.98	14.89	0.00	54.23
B06/220	Engineered	23-Jul-2006	111	71.14	2.68	19.91	2.71	9.95	4.70	0.00
B06/225	Engineered	23-Jul-2006	89	53.79	0.76	31.43	3.37	3.37	20.45	0.00
B06/227	Engineered	25-Jul-2006	73	15.38	3.85	53.79	6.90	4.14	42.31	6.15
B06/204	Engineered	28-Jul-2006	83	60.83	0.00	3.61	4.81	3.61	19.17	11.67
B06/239	Engineered	28-Jul-2006	75	35.66	0.78	21.35	0.00	2.67	30.23	20.16
B06/240	Engineered	28-Jul-2006	92	27.91	0.78	42.41	15.23	10.88	23.26	0.00
B06/289	Engineered	18-Aug-2006	96	74.05	1.53	13.53	4.16	2.08	10.69	0.76
B06/291	Engineered	18-Aug-2006	71	36.19	0.00	26.93	2.83	18.43	30.48	0.00
B06/292	Engineered	19-Aug-2006	86	33.81	2.16	30.13	8.11	19.70	30.22	0.00
B06/310	Engineered	21-Aug-2006	77	4.85	0.61	85.16	2.58	5.16	51.52	0.00
B06/311	Engineered	21-Aug-2006	110	20.48	1.20	74.76	0.00	3.65	25.90	1.81

Table 7. Univariate results for five egg fate categories (addled, embryo, fetus, plant roots, ghost crab) in natural and engineered dunes within Archie Carr National Wildlife Refuge, FL, USA.

Dependent Variable	$F_{1,33}$	p	Dune Type	95% Confidence Interval	
				Lower Bound	Upper Bound
Addled (%)	5.085	0.031	Natural	11.94	28.61
			Engineered	23.92	45.49
Embryo (%)	1.155	0.29	Natural	0.58	4.31
			Engineered	1.85	5.8
Fetus (%)	0.357	0.554	Natural	4.34	10.32
			Engineered	5.29	11.89
Roots (%)	3.005	0.092	Natural	0.41	2.96
			Engineered	0.21	15.74
Ghost Crab (%)	3.402	0.074	Natural	2.91	14.76
			Engineered	9.37	25.8

CHAPTER FOUR: DISCUSSION

Characteristics of nesting beach substrate can affect reproductive success of marine turtles (Crain et al. 1995). Thus, beach restoration projects may affect marine turtle recruitment by altering abiotic conditions of nesting beaches. Restoration projects are necessary to help protect shoreline structures after major erosion events, as was the case in the ACNWR. This restoration project rebuilt dunes to protect private property and provided marine turtle nesting habitat. However, sand for this project was imported from inland quarries, drawing questions as to the suitability of this substrate as an incubation environment marine turtles. My study shows that the abiotic conditions of engineered dunes differed from natural dunes and resulted in lower hatching success of endangered green turtles.

Of the nine characteristics in the backward stepwise regression, only two were significant predictors of hatching success. The date of egg deposition and grain size of the sand surrounding the eggs explained almost 26% of the variation in hatching success. Hatching success decreased as the nesting season progressed and nests laid in the fine-grain sand found predominately on engineered dunes suffered lower rates of hatching than those laid within coarser-grained sand. The net effect reduced hatching success by almost 21% on engineered dunes compared to natural beaches. Thus, using inappropriate sand sources had a significant negative effect on green turtle hatchling production at ACNWR. I estimated that the reduced hatching success found on the engineered dunes at ACNWR resulted in the loss of more than 22,000 endangered green turtle hatchlings.

The mechanism by which sand grain size affected hatching success is uncertain. Altering sand characteristics influences gas exchange and can increase embryonic mortality (Ackerman 1981). Smaller sand grain sizes slow gas diffusion through the substrate, which can limit oxygen availability to the clutch (Ackerman 1977). Poorly sorted sands contain increased amounts of fine and coarse grain sizes, which increase embryonic mortality in green turtles (Mortimer 1990). Natural dunes in this study were moderately to moderately well-sorted, medium sand, while engineered dunes ranged from poorly-sorted, fine sands to moderately-sorted, medium sands. Poorly sorted, fine sands may decrease hatching success in engineered dunes by reducing gas exchange. Physical impediment of gas exchange across the eggshell decreased hatching success in both green turtle (*Chelonia mydas*) and flatback (*Natator depressus*) eggs (Phillott and Parmenter 2001).

Eggs may fail to hatch for multiple reasons. Unfavorable abiotic conditions or disturbances may cause eggs to arrest development early during incubation, resulting in unhatched “addled” eggs. Indeed, there were significantly more addled eggs in engineered dunes compared to natural. Fungal invasions have been known to cause early embryonic death in developing turtles (Phillott et al. 2006), however no fungi on eggs were not noted during this study. Egg consumption by ghost crab predators was higher on engineered dunes relative to natural dunes. Other species of ghost crab have been shown to prefer sand that contain more moisture and may explain this increased activity in engineered dunes (Warburg and Shuchman 1979). In both dune types, ghost crab predation was more prevalent in later season nests.

There are many physical characteristics of a beach that are important for the species that use the habitat (Warburg and Shuchman 1979, Peterson et al. 2000, Peterson and Manning 2001,

Wilber et al. 2003, Fenster et al. 2006, Jackson et al. 2007). Sand compaction can impede a female turtle's ability to dig a nest chamber and the ability of hatchlings to escape the nest (Steinitz et al. 1998, Chen et al. 2007). Reconstructed beaches that have compacted sand can impede a female's ability to dig, altering the shape of egg chambers compared to those of natural beaches, potentially altering incubation environments (Carthy 1996). Nest depth can affect green turtle hatching success (Mortimer 1990), but nest depth did not differ between the two types of dunes. Sand compaction and nest depth may potentially influence the ability of hatchlings to emerge from the nest, however I found no difference in the proportion of hatchlings remaining in inventoried nests between engineered and natural dunes. Sand color has been shown to affect incubation temperature in other sea turtle species (Blair et al. 2000), but I found no difference in incubation temperature between dune types even though sand color differed. This may be because green turtle eggs incubate deeper than other species, insulating the nest from the effects of sand color on nest temperature.

Sand grain size is an important factor in nesting and hatching success, however green turtles tolerate a wide range of sand sizes on natural beaches (Stancyk and Ross 1978, Mortimer 1990, Chen et al. 2007). Grain size influences many parameters important for successful incubation such as porosity, moisture content and sand compactness (Mortimer 1990, Broadwell 1991, Chen et al. 2007). Sand porosity is commonly considered because beach reconstruction decreases the amount of open pore space in sand and affects embryonic development (Ackerman 1981,Carthy 1996). The porosity of the two dune types in this study did not differ, indicating the gaseous environment also was similar. While initial moisture content is not necessarily representative of moisture regime throughout the incubation period, the increased moisture

content in engineered dunes occupies open pore space, reducing the area available for gas. The amount of calcium carbonate in sand is an important component of beach acid–base chemistry. I found less calcium carbonate in the restored dune material than in natural sand but pH did not differ significantly.

My results show that in the restored area of ACNWR, the moderately - sorted fine sand used to build dunes provided a less favorable environment for green turtle embryonic development. In this particular restoration project, the mean grain size of the inland sand did not resemble that of the natural beach, and correlated with reduced green turtle hatchling production. However, the effect of grain size, sorting, and compaction of beach sands are not limited to marine turtles. Many other species inhabiting these beaches, such as ghost crabs and other invertebrates (Jansson 1967, Warburg and Shuchman 1979, Fenster et al. 2006) may be negatively affected by engineered dunes. The endangered northeastern beach tiger beetle (*Cicindela dorsalis dorsalis*) reproduces on the beach and its larval production is sensitive to changes in sand compaction caused by beach restoration (Fenster et al. 2006). Further, restoration may have cascading food web effects by affecting macrofaunal organisms that are prey for surf fish and migratory birds (Peterson and Manning 2001).

Many beach restoration projects have met or exceeded the natural hatching success of other marine turtle species (Broadwell 1991, Iocco 1998, Ecological Associates 1999, Brock 2005, Ehrhart 2005). However, this was not the case for green turtles at ACNWR. Further, if beach restoration continues with inadequate fill material, the potential exists for a variation of an ecological trap to form. In most ecological traps, it is some anthropogenic characteristic of a poor habitat that attracts an individual to it (Battin 2004). In the case of green turtles, it is their

strong nest site fidelity that brings them back to the same nesting beaches year after year (Meylan et al. 1990). The continued improper reconstruction of these beaches leaves females to nest in sand that will ultimately lower future recruitment due to their biological predisposition to return to these areas. However, measuring this kind of effect on such a long-lived animal is difficult and quantifying long term effects are nearly impossible (Musick 1999).

Beach erosion is a natural process. However, human development and structures preclude the natural processes of erosion and accretion that have historically maintained beaches (Nordstrom 2005). Thus, beach restoration's main goal is anthropogenic: providing an unending patch of sand on which erosion may operate rather than fixing the ultimate problem of structures that impede coastal movement (Frazer 1992). In this dune restoration project, the urgency to protect private property overwhelmed the policy designed to protect the beach environment, which had direct consequences for the endangered green turtle. My work shows the sand source chosen had direct, negative effects on the green turtles at ACNWR and reinforces the need for maintaining standards when selecting fill material for beach restoration projects.

APPENDIX: DATA LOGGER PREPARATION

I measured hourly incubation temperatures using Hobo H8 temperature data loggers (Onset Computer Corporation 2002) placed in the middle of the egg mass. Placing the data logger in the center of the clutch gives a representative temperature estimate of all eggs within the egg chamber (Hanson et al. 1998). I vacuum sealed data loggers (Foodsaver vac 200, New York) in pouches containing a small desiccant container (Hanson et al. 1998).

I initially calibrated data loggers using an ice bath, which was measured every 5 min. for 4h using a digital thermometer (Omega HH - 25TC; range -80°C – 400° C). I compared the digital temperature to that recorded on the data logger to determine the calibration factor for each logger. After data loggers were retrieved, I calibrated 29 of the 40 again in an ice bath and at a temperature range typically found in nests (25 °, 28 °, 31° and 34 ° C) to ensure loggers were accurate to factory standards (± 0.7 ° C). Raw data were close to temperatures predicted by each logger's calibration curve (log likelihood test Chi-square = 8.278, $p = 0.004$).

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